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A Molecular Phylogeny of *Macaca* Based on Mitochondrial Control Region Sequences

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Abstract: Nucleotide sequences of segments of the mitochondrial control regions were analyzed to infer the phylogenetic relationships among 7 macaques. High nucleotide diversity in *Macaca assamensis* and relatively low diversity in *M. thibetana* were found. Based on the ML tree from control regions, species in our study can roughly be sorted into three species groups except for the phylogenetic position of *M. fascicularis*, i.e., *silenus* group, including *M. leonina*; *sinica* group, including *M. arctoides*, *M. assamensis*, and *M. thibetana*; and *fascicularis* group, including *M. mulatta* and *M. cyclopis*. A discrepancy between earlier studies (Fooden & Lanyon, 1989; Tosi et al, 2003a; Deinard & Smith, 2001; Evans et al, 1999; Hayasaka et al, 1996; Morales & Melnick, 1998), our result supported the hypothesis that *M. fascicularis* diverged earlier than *M. leonina*. Mitochondrial paraphyly in eastern *M. mulatta* (with respect to *M. cyclopis*) and eastern *M. assamensis* (with respect to *M. thibetana*) were clearly observed in our study. In accordance with the results of Y chromosome, allozyme, nuclear genes and some morphological data (Delson, 1980; Fooden & Lanyon, 1989; Fooden, 1990; Tosi et al, 2000, 2003a, b; Deinard & Smith, 2001), our study on control region sequences supported *M. arctoides* to be classified into the *sinica* group. However, this result disagreed with the previous mtDNA studies (Hayasaka et al, 1996; Morales & Melnick, 1998; Tosi et al, 2003a).

Key words: *Macaca*; Macaque; Mitochondrial DNA; Control region; Phylogeny

基于线粒体控制区序列的猕猴属系统发育研究

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摘要: 通过线粒体部分控制区 DNA 序列数据探讨 7 种猕猴属物种的分子系统发育关系。结果表明熊猴的核苷酸多样度最高, 而藏酋猴核苷酸多样度较低。基于控制区序列数据所构建的最大似然树, 不考虑食蟹猴的位置, 7 种猕猴物种可粗略地分为 3 个种组, 即狮尾猴组 (包括北平顶猴)、头巾猴组 (包括红面猴、熊猴和藏酋猴) 和食蟹猴组 (包括恒河猴和台湾猴)。与前人 (Fooden & Lanyon, 1989; Tosi et al, 2003a; Deinard & Smith, 2001; Evans et al, 1999; Hayasaka et al, 1996; Morales & Melnick, 1998) 的结果不同, 我们的结果支持食蟹猴比北平顶猴分化早的假设; 东部恒河猴 (相对于台湾猴) 和东部熊猴 (相对于藏酋猴) 出现并系。与 Y 染色体、等位酶、核基因以及部分形态学数据推测的结果 (Delson, 1980; Fooden & Lanyon, 1989; Fooden, 1990; Tosi et al, 2000, 2003a, b; Deinard & Smith, 2001) 一致, 红面猴应归于头巾猴组, 但此结论与前人 (Hayasaka et al, 1996; Morales & Melnick, 1998; Tosi et al, 2003a) 依据线粒体得到的结果有较大分歧。

关键词: 猕猴属; 猕猴; 线粒体 DNA; 控制区; 系统发育

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The genus *Macaca* is the most widely distributed non-human primates with its 19 extent species extending from northwestern Africa to a number of islands and continental areas in southern and eastern Asia (Groves, 2001; Abegg & Thierry, 2002).

On the basis of male genitalia, Fooden (1976) classified the macaques into four species groups: *silenus-sylvanus* group, including *M. sylvanus*, *M. silenus*, *M. nemestrina* and the Sulawesi macaques; *sinica* group, including *M. sinica*, *M. radiata*, *M. assamensis*, and *M. thibetana*; *arctoides* group, including *M. arctoides*; and *fascicularis* group, including *M. fuscata*, *M. mulatta*, *M. cyclopis*, and *M. fascicularis*. However, Delson (1980) established his classification system with a little difference: *M. arctoides* falled within the *sinica* group and *M. sylvanus* formed its own group. The viewpoint had been supported by many followers (Nozawa et al, 1977; Cronin et al, 1980; Melnick & Kidd, 1985; Fooden & Lanyon, 1989; Tosi et al, 2000, 2003a; Deinard & Smith, 2001). However, Groves (2001) divided the genus into six species-groups based on morphologic traits: 1) *M. sylvanus* group: monotypic; 2) *M. nemestrina* group: *M. nemestrina*, *M. leonina*, *M. silenus* and *M. pagensis*; 3) Sulawesi group; 4) *M. fascicularis* group: *M. fascicularis* and *M. arctoides*; 5) *M. mulatta* group: *M. fuscata*, *M. mulatta* and *M. cyclopis* and 6) *M. sinica* group: *M. sinica*, *M. radiata*, *M. assamensis*, and *M. thibetana*. Zhang & Shi (1993) recovered Fooden's classification with the help of mtDNA restriction analyses. Furthermore, the result of Morales & Melnick (1998) was less concordant with the separation of the species into four distinct species groups. In the tree based on mtDNA sequences, the bootstrap values of some clades were too low (< 50%) (Hayasaka et al, 1996; Tosi et al, 2003a). Therefore, further investigation and more data of mtDNA will be useful to resolve these problems. In the present study, we analyzed segments of the control region sequences to obtain further insights into the phylogenic relationships of genus *Macaca*.

1 Materials and Methods

1.1 Materials

thirty-eight individuals representing 7 species: *M. cyclopis*, *M. leonina*, *M. thibetana*, *M. assamensis*, *M. arctoides*, *M. mulatta*, and *M. fascicularis* (Table 1) were investigated. Baboon was served as the outgroup. Total genomic DNA was extracted from whole blood or other tissues using the standard phenol/chloroform protocols.

1.2 MtDNA sequencing

The mtDNA control region was amplified using the PCR primer LqqF (TCCTAGGGCAATCAGAAAGAAAG) and TDKD (CCTGAAGTAGGAACCAGATG). Each mixture contained at least 25 ng DNA template, 5 μL 10 × reaction buffer, 1 pmol/L forward and reverse primer, 2 mmol/L mixed DNTP, 3 mmol/L $MgCl_2$, 0.25 unit of Taq polymerase enzyme, adding sterile distilled water to 50 μL and overlaid with mineral oil. Amplification was performed on a RoboCycler Gradient 40 (Stratagene) thermal cycler.

The cycling conditions for all markers began with an initial 2 min denaturation at 95 ℃; followed by 35 cycles of 1 min denaturation at 94 ℃, 1 min annealing at 60 ℃ and 1 min of extension at 72 ℃; a 5 min final extension at 72 ℃ concluded each reaction.

The PCR products were tested using agarose gel electrophoresis and purified with the Gel Extraction Mini Kit of Warson Co. (Shanghai, China) following the manufacturer's instructions. Purified PCR products were labeled using the BigDyeTM Terminator cycle sequencing kits (PE Biosystems, Foster City, CA) with an ABI 377DNA automatic sequencer using the same primers as used in the PCR reactions. Cycle sequencing reactions were performed following the instructions provided by the manufacturer. Both forward and reverse directions were sequenced.

DNA sequences were edited using DNASTAR (DNASTAR Inc.) and aligned by CLUSTAL W program (Thompson et al, 1994).

1.3 Data analyses

Base compositional information and the nucleotide diversity (π value) for control region were estimated by MEGA 2.1 (Kumar et al, 2001). TREE-PUZZLE (Strimmer & von Haeseler, 1996) was used to construct a maximum-likelihood (ML) tree for the sequence data. An optimal model that fit the data for ML trees was determined by using Modeltest 3.0 (Posada & Crandall, 1998). HKY + G was the most appropriate for ML analysis. Settings for the HKY + G

Table 1 Samples used in this study and nucleotide diversity within each taxon

No.	Samples	Origin	Origin abbr.	GenBank no.	Samples size	π value[1] (%)
1	*M. cyclopis*	Taiwan	TW	AY682594	1	*
2	*M. arctoides*	Yunnan, China	YN	AY682588	6	4.1
3	*M. arctoides*	Yunnan, China	YN	AY682589		
4	*M. arctoides*	Vietnam	V	AY682591		
5	*M. arctoides*	Vietnam	V	AY682592		
6	*M. arctoides*	South of China	SO	AY682590		
7	*M. arctoides*	Yunnan, China	YN	AY682593		
8	*M. assamensis*	Vietnam	V	AY682611	12	5.9
9	*M. assamensis*	Vietnam	V	AY682613		
10	*M. assamensis*	Vietnam	V	AY682617		
11	*M. assamensis*	Yunnan, China	YN	AY682614		
12	*M. assamensis*	Yunnan, China	YN	AY682615		
13	*M. assamensis*	Yunnan, China	YN	AY682616		
14	*M. assamensis*	Yunnan, China	YN	AY682612		
15	*M. assamensis*	Myanmar	MY	AY682619		
16	*M. assamensis*	Myanmar	MY	AY682621		
17	*M. assamensis*	Myanmar	MY	AY682620		
18	*M. assamensis*	Myanmar	MY	AY682622		
19	*M. assamensis*	South of China	SO	AY682618		
20	*M. fascicularis*	Vietnam	V	AY682595	4	3.4
21	*M. fascicularis*	Vietnam	V	AY682596		
22	*M. fascicularis*	Vietnam	V	AY682597		
23	*M. fascicularis*	Vietnam	V	AY682598		
24	*M. thibetana*	Sichuan, China	SC	AY682610	5	0.6
25	*M. thibetana*	Sichuan, China	SC	AY682607		
26	*M. thibetana*	Sichuan, China	SC	AY682608		
27	*M. thibetana*	Sichuan, China	SC	AY682609		
28	*M. thibetana*	Sichuan, China	SC	AY682606		
29	*M. leonina*	South of China	SO	AY682623	4	5.6
30	*M. leonina*	South of China	SO	AY682624		
31	*M. leonina*	Yunnan, China	YN	AY682625		
32	*M. leonina*	Myanmar	NY	AY682626		
33	*M. mulatta*	Fujian, China	FJ	AY682600	6	4.5
34	*M. mulatta*	Fujian, China	FJ	AY682599		
35	*M. mulatta*	Fujian, China	FJ	AY682601		
36	*M. mulatta*	Fujian, China	FJ	AY682602		
37	*M. mulatta*	Yunnan, China	YN	AY682603		
38	*M. mulatta*	Guizhou, China	GZ	AY682604		
39	*Papio*	Africa	AF	AY682605	1	*

[1] Kimura-2-parameter model was used for mtDNA data analysis; * Species with one sample was omitted in the present study.

model were as follows: $-\ln L = 3428.3647$; base frequencies = (A = 0.3253, C = 0.2825, G = 0.1222, and T = 0.2699), Ti/tv ratio = 11.9858, and the shape parameter of the gamma distribution = 0.2221.

2 Results and Discussion

Thirty-nine individuals were successfully sequenced and 33 haplotypes were identified. Sequences had been deposited into GenBank (Table 1). The strong bias against guanine was observed in our amplified sequences (G = 12.8%, A = 31.1%, C = 28.7%, T = 27.4%), which characterized mtDNA rather than Numts (the nuclear insertions of mtDNA sequences). In the 541 bp sequences of the control regions, a total of 230 variable sites and 174 parsimony informative sites had been found. The nucleotide diversity (π value) of control region in *M. assamensis* was slightly higher than in any other species, however, *M. thibetana* showed a relatively low diversity (Table 1).

As illustrated by the ML tree based on control regions (Fig.1), except for *M. assamensis* and *M. mulatta*, the different haplotypes found within a single species generally clustered together on a branch

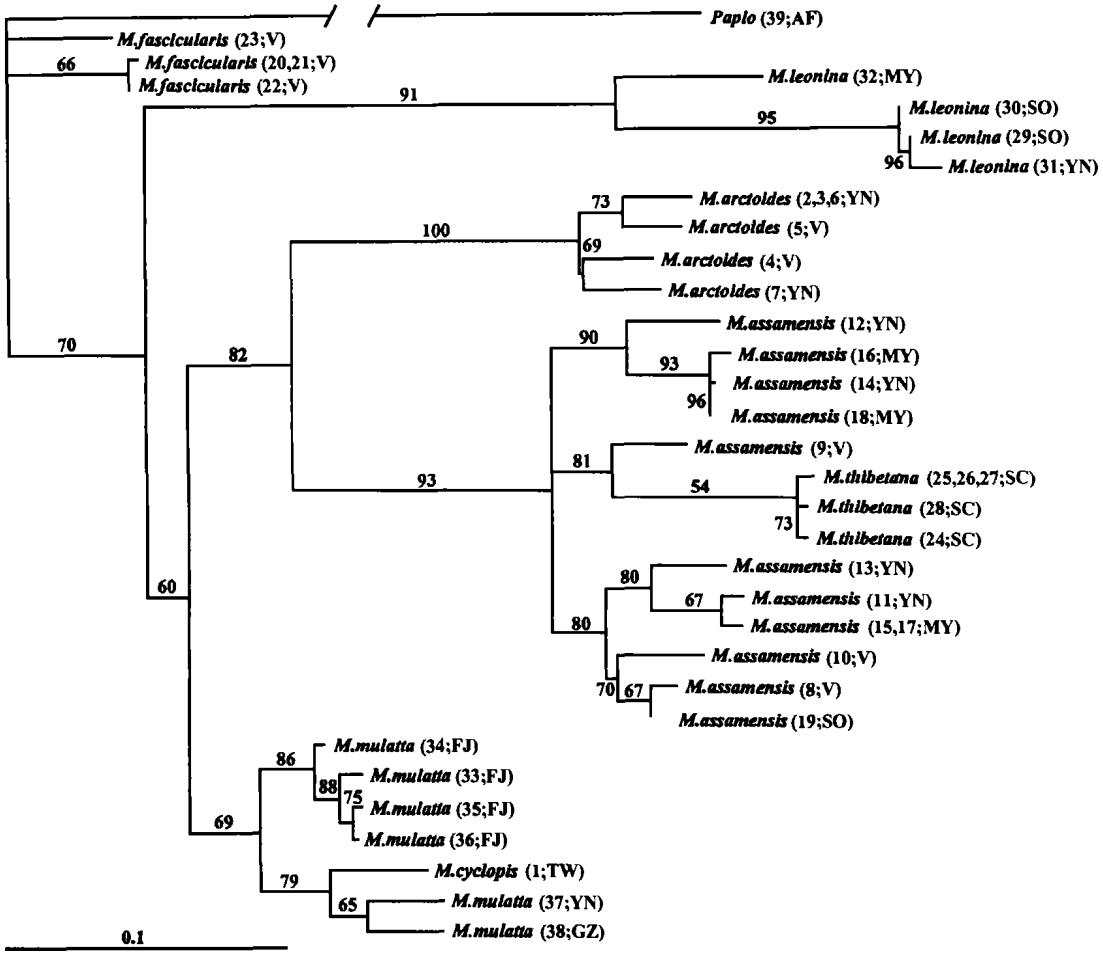

Fig.1 The maximum-likelihood (ML) tree based on control region sequences used by TREE-PUZZLE
Only reliability percentages (after 1 000 quarter puzzling steps) above 50% are indicated. Numbers and letters in parentheses correspond to sample identifications and origin abbreviation outlined in Table 1.

of the tree that did not include any haplotypes from other species. Contrasting with the classification system of Delson (1980), species examined could roughly be divided into three species group except for the phylogenetic position of *M. fascicularis*: *silenus* group, including *M. leonina*; *sinica* group, including *M. arctoides*, *M. assamensis*, and *M. thibetana*; and *fascicularis* group, including *M. mulatta* and *M. cyclopis*. A discrepancy with earlier studies (Fooden & Lanyon, 1989; Tosi et al, 2003a; Deinard & Smith, 2001; Evans et al, 1999; Hayasaka et al, 1996; Morales & Melnick, 1998), *M. fascicularis* diverged early in our ML tree based on control region with low reliability support (70%, Fig.1).

Two macaque species were paraphyletic in this study: *M. mulatta* (with respect to *M. cyclopis*) and *M. assamensis* (with respect to *M. thibetana*). Previous mtDNA studies had suggested a paraphyletic status for particular macaque species, for example, *M. assamensis* (Hoelzer et al, 1992), *M. mulatta* (Melnick et al, 1993; Hayasaka et al, 1996; Morales & Melnick, 1998; Tosi et al, 2002, 2003a) and *M. nemestrina* (Evans et al, 1999). In the paraphyly of *M. mulatta* (with respect to *M. cyclopis*) and *M. assamensis* (with respect to *M. thibetana*), earlier studies (Hoelzer et al, 1992; Melnick et al, 1993; Hayasaka et al, 1996; Morales & Melnick, 1998; Tosi et al, 2002, 2003b) suggested a major separation between the eastern and the western lineages of *M. mulatta* and *M. assamensis* occurring along the Bramaputra river valley. The eastern *M. mulatta* lineage was more closely related to the *M. cyclopis* than to the western lineage. *M. assamensis* was composed of eastern and western sub-species: *M. a. assamensis* and *M. a. pelops*, respectively (Fooden, 1982). Hoelzer et al (1992) documented that the eastern *M. assamensis* lineage (*M. a. assamensis*) was more closely related to

M. thibetana than to the western lineage (reviewed in Hoelzer & Melnick, 1996).

Our results, however, was entirely out of expectation. In this study, we just had the eastern samples of *M. mulatta* and *M. assamensis*. *M. mulatta* and *M. assamensis* were still paraphyletic with respect to *M. cyclopis* and *M. thibetana*. *M. mulatta* cluster (including *M. cyclopis*) clearly diverged into two main clades. *M. mulatta* of Fujian origin (eastern) diverged first and formed one clade. The other clade contained *M. cyclopis* and *M. mulatta* of Yunnan and Guizhou origins (eastern). The departure from intraspecific monophyly was seen at its most extreme in the case of *M. assamensis*. Twelve individuals were successfully sequenced and three main clades have been occurred among them. The samples collected from the same place did not define an exclusive clade. Three *M. thibetana* haplotypes derived from five samples grouped an independent branch and swamped into the *M. assamensis* haplotypes. We could not continue further addressing about the paraphyly mechanism of *M. mulatta* and *M. assamensis* because we were short of the western *M. mulatta*, western *M. assamensis* (*M. a. pelops*) lineages and other species within the *fascicularis* group and the *sinica* group. Additional work should be carried out in future.

It was noteworthy that *M. arctoides* and *M. assamensis/M. thibetana* are clustered (Fig. 1), which echoed the results of Y chromosome, allozyme, nuclear genes and some morphological data (Delson, 1980; Fooden & Lanyon, 1989; Fooden, 1990; Tosi et al, 2000, 2003a, b; Deinard & Smith, 2001), in which *M. arctoides* had been put into the *sinica* group (*M. assamensis* and *M. thibetana* in this study). However, the result disagreed with the previous mtDNA (Hayasaka et al, 1996; Morales & Melnick, 1998; Tosi et al, 2003a) and morphological studies of Groves (20001). They all infered a closely affinity of *M. arctoides* to the *fascicularis* group members (*M. fascicularis*, *M. mulatta* and *M. cyclopis* in this study) or *M. fascicularis*. It had been argued that genes evolved under different evolutionary rates and constraints resulted in very different topologies (Bull et al, 1993; de Queiroz et al, 1995). Control region exhibits a higher rate of nucleotide substitution than protein coding (ND4/ND5 used in Hayasaka et al, 1996) and RNA genes (12*S*/16*S* rRNA used in Morales & Melnick, 1998; Tosi et al, 2003a). Further studies with more sequences are required to resolve these problems.

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